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Research Article

An integrative framework to assess the spatio-temporal impact of plant invasion on ecosystem functioning

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Abstract

Invasive species can alter the structure and functioning of the invaded ecosystem, but predictions of the impact of invasive species on ecosystem functioning are weak. Invasion is determined by the interplay of invasive species traits, the recipient community, and the environmental context. However, efficient approaches to assess the spatial dimension of functional changes in heterogeneous environments and altered plant-plant interactions are lacking. Based on recent technological progress, we posit a way forward to i) quantify the fine-scale heterogeneity of the environmental context, ii) map the structure and function of the invaded system, iii) trace changes induced by the invader with functional tracers, and iv) integrate the different spatio-temporal information from different scales using (artificial intelligence-based) modelling approaches to better predict invasion impacts. An animated 3-D model visualisation demonstrates how maps of functional tracers reveal spatio-temporal dynamics of invader impacts. Merging fine- to coarse-scale spatially explicit information of functional changes with remotely sensed metrics will open new avenues for detecting invader impacts on ecosystem functioning.

Key words: community structure, environmental context, functional tracer, invader-ecosystem interaction, remote sensing, spatio-temporal heterogeneity, spatio-temporal modelling

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Introduction

Biological invasions of non-native species pose a large threat to biodiversity (IPBES 2019). Many invasive plant species significantly alter the biophysical and biochemical environment, thereby facilitating their own growth (Gaertner et al. 2014), with cascading effects on the structure and functioning of the invaded ecosystems. However, mechanisms of invader impact can be manifold (Ehrenfeld 2010; Sapsford et al. 2020), and challenges to quantify impact occur due to the multiplicity of invading species, context-dependencies, and interactions, as well as intraspecific trait variation (Sapsford et al. 2020). Predicting the effects of biological invasions on ecosystem functioning and services is of uttermost importance for prioritizing management and anticipating undesirable consequences of invasions (Simberloff et al. 2013; Jeschke et al. 2014; Brundu et al. 2020; Essl et al. 2020; Kumschick et al. 2020; Pyšek et al. 2020b; Ricciardi

et al. 2021; Gallardo et al. 2024; Vilà et al. 2024). To date, multiple hypotheses and concepts have been developed that capture different aspects of invasion impact, habitat invasibility, and species' invasiveness (Hobbs and Humphries 1995; Alpert et al. 2000; Whitney and Gabler 2008; Enders et al. 2020; Novoa et al. 2020; Catford et al. 2021; Cavieres 2021; Hui et al. 2023), although data to thoroughly test these are often scarce (Gioria et al. 2023).

The ecological impact of invasive species depends on direct interactions between native and invasive plants, which in turn are influenced by native and invasive species' traits (Pyšek et al. 2012, 2020a; Sapsford et al. 2020), or trait differences between both groups (Castro-Díez et al. 2014; Lee et al. 2017; Kuebbing et al. 2018; Dyderski and Jagodziński 2019). Consequently, there is increasing awareness of the relevance of interactions and dynamics for invasion success, such as the interplay between invading species' traits and the recipient ecosystem (Kueffer et al. 2013; Kumschick et al. 2015; Sardans et al. 2017; Novoa et al. 2020). However, new approaches are needed to quantitatively assess these interactions (Gioria et al. 2023).

Species interactions as well as plant-soil feedbacks take place on a spatially confined scale within centimetres to metres in the neighbourhood of the invader (Mitchell et al. 2006), which is further referred to as fine-scale. While the temporal aspect of such feedbacks has been documented (Yelenik and D'Antonio 2013; Gioria and Osborne 2014), studies on impacts at plant-individual scale are clearly underrepresented (Crystal-Ornelas and Lockwood 2020). The spatial arrangement and distribution of native and invasive species is a decisive factor determining whether individuals interact and, potentially, which type of interaction – i.e., competition or facilitation – dominates (Hellmann et al. 2016a, 2016b; Cavieres 2021).

In addition, there is growing recognition that the effect of the invasive species is influenced by the environmental conditions, such as microclimatic or local edaphic conditions (Sapsford et al. 2020; Catford et al. 2021). The environmental context, namely the fine-scale spatial heterogeneity of abiotic and biotic conditions, is an important but often neglected dimension (Jarić et al. 2019; Fenesi et al. 2023), and the spatio-temporal variation of a system is a major source of uncertainty of impact assessments (Probert et al. 2020). Local availability of resources, such as water, nutrients or light, can shift the competitive balance between invasive and native species (Werner et al. 2010; Soliveres et al. 2015; Alba et al. 2019; Haberstroh et al. 2021). Therefore, predicting ecological impacts of invasive species considering context-dependency is still a major challenge (Ricciardi et al. 2021).

We posit that spatio-temporal heterogeneity can represent an environmental property in itself, which can affect invasibility, or else be affected by invasion, and requires better inclusion in invasion ecology. In the past, progress was hampered by a lack of methodological approaches, but now significant progress, e.g. in remote sensing technology, allows capturing high-resolution information on environmental heterogeneity at fine scales where plant-plant interactions take place.

Hence, we advocate combining advances in various disciplines of ecophysiology, invasion ecology, remote sensing, mapping, and modelling. This will open new opportunities to characterize environmental heterogeneity and associated changes in invasive-native species interaction at high-spatiotemporal resolution to better predict invasion dynamics and impact, as outlined in the following.

Concept for integrating fine-scale environmental heterogeneity and functional changes into spatial models of invader-ecosystem interactions

Direct interactions between the invasive and native species, such as above- or belowground facilitation or competition for e.g. resources, spaces, or pollinators will determine the invaders' successful establishment and growth (Fig. 1). These direct interactions are embedded in the environmental context, which is likewise shaping the competitive balance if conditions favour either native or invasive substitute by species. The competitive balance may even shift between competition and facilitation under changing environmental conditions or extreme climatic events (Werner et al. 2010; Grossiord 2020; Cavieres 2021; Haberstroh and Werner 2022). Inversely, some invaders can change environmental properties through positive- or negative feedback loops, thereby often promoting their own invasion success, which can ultimately result in regime shifts (Gaertner et al. 2014) and potentially magnify the impact beyond direct competition through cascading effects (Carboni et al. 2021). Currently, there exists a robust theoretical framework addressing the success of invasiveness as a result of direct and indirect interactions and the interplay between species traits, as well as on the recipient community structure and functioning and the environmental context (Gaertner et al. 2014; Novoa et al. 2020; Pyšek et al. 2020a; Hui et al. 2023; summarized in Fig. 2).

However, detecting and tracing the impacts of invasive species in natural environments have been hindered in the past due to a lack of suitable measurements and integration methods to explicitly quantify the spatio-temporal dimensions involved. This would require not only mapping the invasive species and its spread in natural systems, but also quantifying local changes in different abiotic and biotic processes that are altered by the invader (i.e. quantifying the local impact of the invader). As the latter is a function of both the environmental conditions and the structure and functioning of the native community, both need to be quantified at high spatio-temporal resolution. For each of these aspects, the required tools are at hand, but new integrative analyses are required.

Hence, we posit a way forward (Fig. 3) on how to i) quantify the fine-scale heterogeneity of the environmental context, ii) map the structure and function of the invaded system, iii) trace changes induced by the invader with functional tracers, and iv) apply effective approaches for integration of spatio-temporal information from different scales, e.g. via different (artificial intelligence-based) modelling approaches, for better prediction of invasive species impact.

Figure 1. Invasive species directly interact with native species by competition or facilitation e.g. for above and belowground resources, thereby changing the biotic and abiotic environment locally.

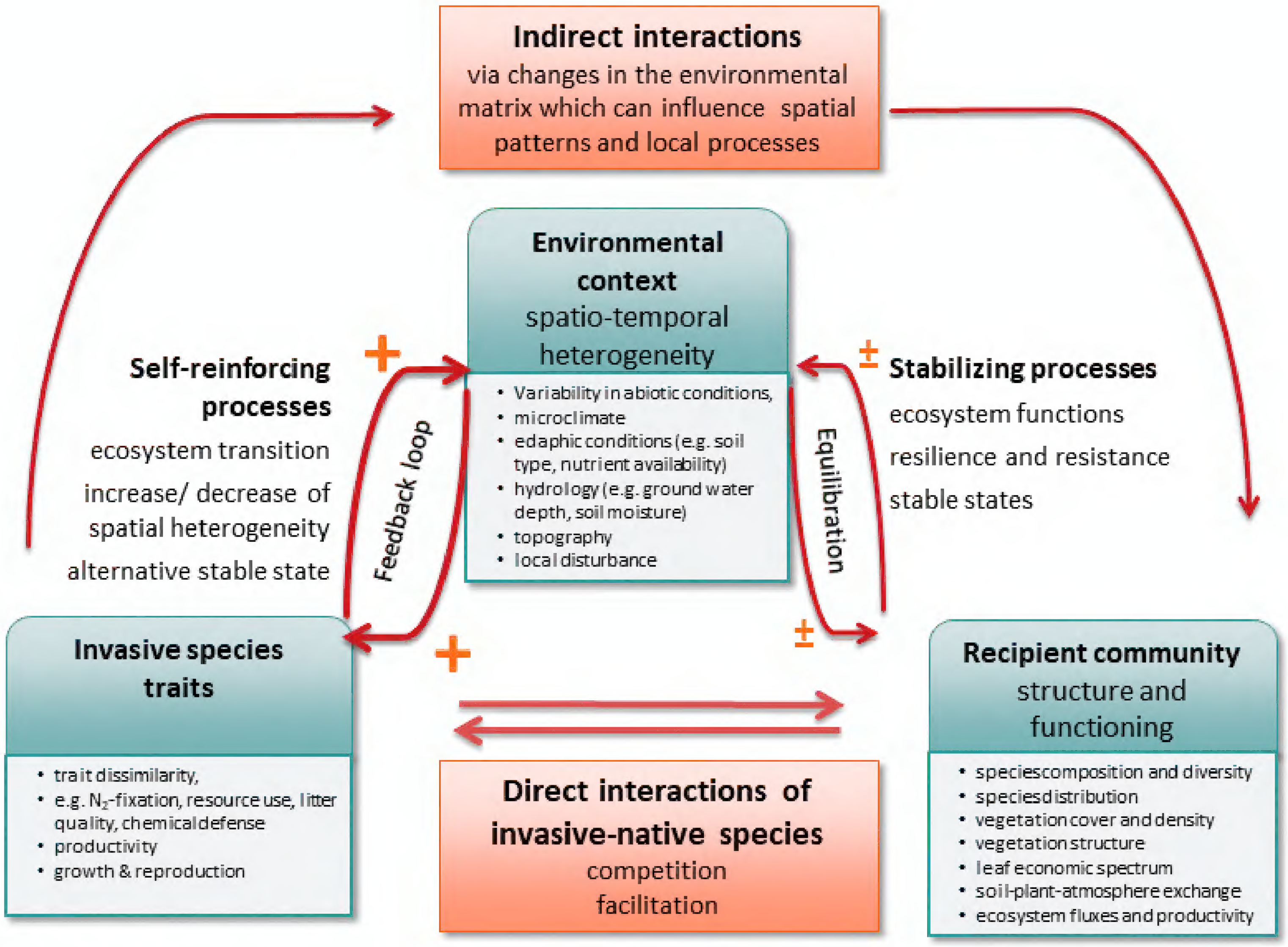

Figure 2. Mechanisms determine plant invasion impact. Plant invasion impact results from direct and indirect interactions between invasive and native species based on the interplay between invasive species traits, structure and function of the recipient community, and spatio-temporal heterogeneity of the environment. Direct interactions between invasive and native species result from competition or facilitation, e.g. for resources, whereas indirect interactions are mediated via subsequent changes in the biotic and abiotic environment, which may favour self-reinforcing processes of the invader or stabilizing processes of the community. Examples of important factors for each category are given in the boxes.

Environmental context

The environmental context is defined as the biogeochemical and physical matrix, which provides the background for both native and invasive species' biotic interactions (Fig. 3). This includes the fine-scale spatio-temporal heterogeneity in, e.g. abiotic conditions like hydrological and edaphic conditions or microclimate, as well as resource patches, e.g. after local disturbance. On the scale of centimetres to kilometres, variation in these conditions can influence plant performance and interactions, thereby creating a multi-layered mosaic of background conditions. An inherent challenge of geospatial analysis is that fine-scale or high resolution data are often collected over small areas, while for large areas only coarse-scale data are available (Millington 2021). However, research rapidly advances regarding the retrieval of two- and three-dimensional geospatial information on the environmental matrix using sensory networks (Allan et al. 2018; Lahoz-Monfort and Magrath 2021; Besson et al. 2022; Sethi et al. 2022) and remote sensing (Lausch et al. 2020; Lahoz-Monfort and Magrath 2021; Skidmore et al. 2021; Timmermans and Kissling 2023). Currently, a broad set of novel digital tools to describe the environmental context is emerging, including UAVs (Unmanned Aerial Vehicles), microsatellites (e.g. PlanetScope), active sensor systems based on LiDAR (Light Detection and Ranging) or SAR (Synthetic Aperture Radar) technology for vegetation structure analysis, and advanced versions of the established Landsat and Sentinel-2 satellites (Crowley and Cardille 2020).

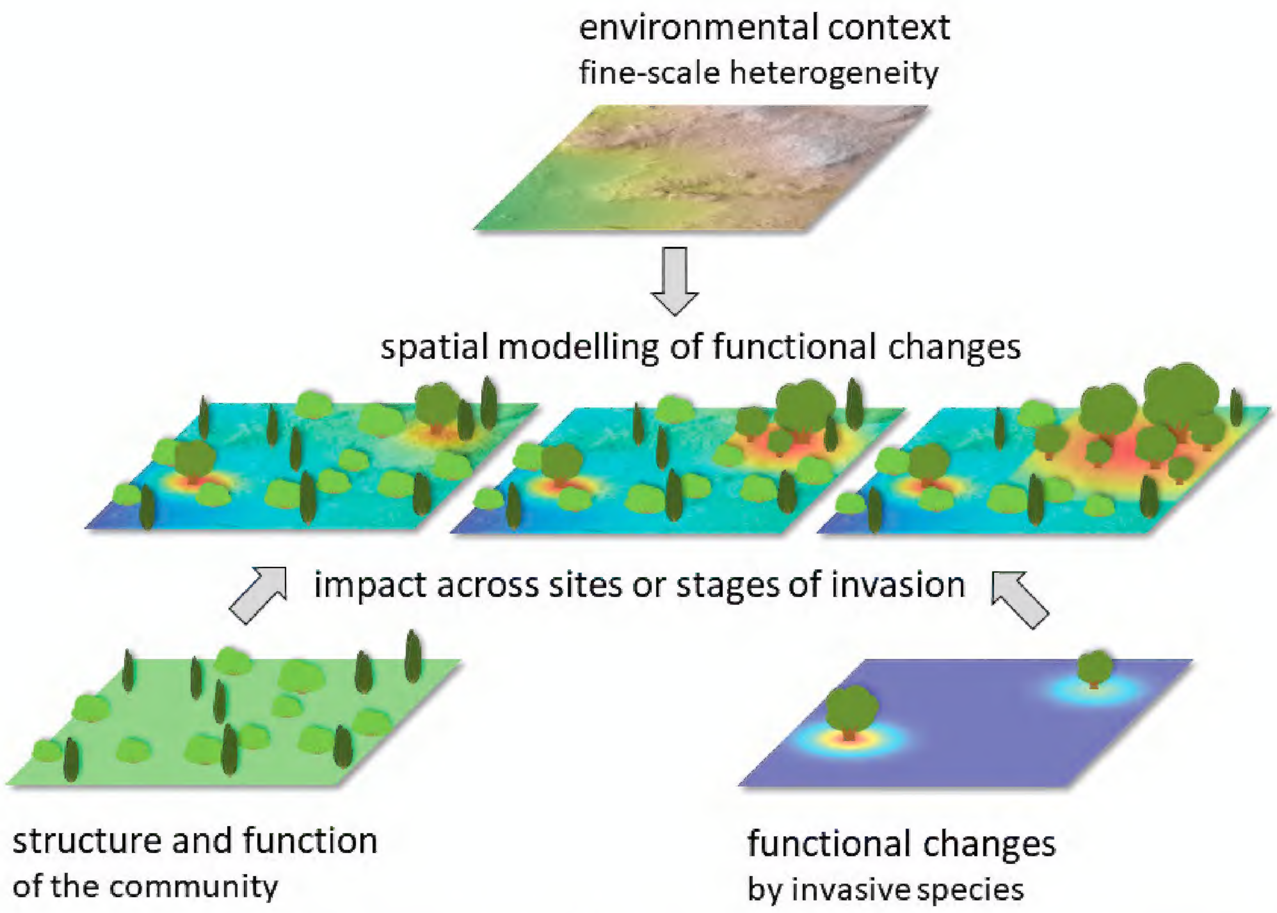

Figure 3. Framework for integrating fine-scale environmental heterogeneity and functional changes into spatial models of invader-ecosystem interactions. Maps of biochemical and biophysical heterogeneous environments can be directly incorporated into predictive models of impact measures across different sites or stages of invasion. Essential complementary spatial data include the location of the invasive species, maps of functional tracers that reflect local changes in key functions induced by the invader, and maps of the recipient community structure and function (e.g. Hellmann et al. (2017)). Technological advances in measurement techniques, sensor networks, and remote sensing will facilitate the collection of high-resolution data on the environmental context, the invasive species, and the recipient community, thereby improving the understanding of invasion dynamics and processes, particularly at the neighbourhood scale.

Structure and function

The environmental context further shapes native species distribution patterns as well as structure and function of the community. Indeed, spatial complexity, in which invasive species interactions take place, can be a proxy for ecosystem structure and dynamics in itself (Parrott 2010). Similarly to assessing the environmental conditions, advances in remote sensing techniques allow for multiscale and multi-temporal mapping of species distribution, and landscape structure and function (Crowley and Cardille 2020), which are exceptionally valuable to describe both the environmental context and structure of the recipient community. LiDAR, SAR, and digital aerial photogrammetry hold great potential to describe ecosystem structural parameters such as vegetation height, cover, density, structural complexity, and population structure (Valbuena et al. 2020). Proofs-of-concept exist for high-resolution automated structural measurements (Calders et al. 2023), while both active and passive sensor systems can be used to map ecosystem functions (Pettorelli et al. 2018).

Moreover, spatially explicit maps of the invader are required, as impact is related to abundance in various forms (Sofaer et al. 2018; Strayer 2020; O'Loughlin et al. 2021). Access to spatial data on invasive plant distribution is improving (Fusco et al. 2023), and distribution maps of the invader can be created and updated across scales using data from UAS (Uncrewed Aerial Systems), aircrafts, and satellites (Vaz et al. 2018; Timmermans and Kissling 2023). Freely available earth observation data are extremely useful to produce such distribution maps, particularly in data poor regions (Truong et al. 2017). Novel approaches to map invasive species and characterize the species composition of the recipient community include methods of Deep Learning (DL) and other methods of machine learning. In invasion ecology, the potential use

of DL is manifold (Christin et al. 2019; Hirn et al. 2022; Perry et al. 2022), but its main application is probably species identification and mapping (Christin et al. 2019; Kattenborn et al. 2021; Borowiec et al. 2022; Müllerová et al. 2023).

Functional tracers of invader impact

Ultimately, the impact of the invader, i.e. its effect on the biophysical, biochemical, and biological environment, has to be assessed. One effective way to quantify invasive species impact is the use of functional tracers, which reflect local changes in key functions at fine spatio-temporal scales. The choice of suitable tracers will depend on both the invasive species under study and invaded community properties, and should capture the processes likely altered by the invasive species, for example nitrogen for N-fixing invaders in N-poor environments or water balance for water-spending invaders in water-limited systems (Fig. 2). Stable isotopes, for example, can provide such functional or ecophysiological tracers, as they reflect changes in interactions and altered functional processes at fine spatial resolution (Cheesman and Cernusak 2016), and provide great potential to unravel mechanisms of invasions (McCue et al. 2020). Applied in a spatially explicit manner (i.e. isoscapes (Rascher et al. 2012)), they can trace local changes in plant-plant interaction and in environmental conditions (Hellmann et al. 2017). Maps can be generated for isotopic measurements of the soil environment or leaves of different native species, thereby directly mapping the invader impact on these species (Hellmann et al. 2016a, 2016b; Nielsen et al. 2016; Sena-Souza et al. 2023). For example, atmospheric N_2-input by N-fixing invaders can be traced into the native vegetation by nitrogen isotopes ($\delta^{15}N$, example in Fig. 3). These changes can lead to cascading effects on other ecosystem functions. Besides nutrient cycling, subsequent changes, e.g. in water and/or carbon cycles, may also be involved (Le Maitre et al. 2015; Dzikiti et al. 2017). Competition for water can affect the water-use-efficiency and hydraulic regulation of native species (Haberstroh et al. 2021), with cascading effects on ecosystem water balance (Rascher et al. 2010; Caldeira et al. 2015; Le Maitre et al. 2020). Changes in native species' carbon isotope ratio ($\delta^{13}C$) can resolve changes in water use efficiency in response to competitive or facilitative invader interactions (Hellmann et al. 2016a; Crous et al. 2019; Sena-Souza et al. 2023). Even shifts between facilitation and competition with increasing distance to the invader have been observed (Hellmann et al. 2016a).

Different tracers can be combined (Funk et al. 2017), such as C, N, P concentrations or other biochemical properties that may be affected by the invasion (Drenovsky et al. 2012; Hellmann et al. 2016a; Helsen et al. 2020; Sena-Souza et al. 2023) or which might reveal functional differences (Große-Stoltenberg et al. 2018b; Meira-Neto et al. 2023) along environmental gradients (Crous et al. 2019). Thereby, differences in the spatial dimension of impact can be revealed both between native and invasive species, depending on their susceptibility to these changes, and with respect to different processes involved.

Remote sensing techniques have also proven invaluable in examining functional properties of invasive species (Helsen et al. 2020; Andrew et al. 2014; Dzikiti et al. 2016; Große-Stoltenberg et al. 2018a, 2018b; Ewald et al. 2018; Hacker and Coops 2022; Große-Stoltenberg et al. 2023) as well as plant-plant interactions (Chen et al. 2022). Further, first studies show that mycorrhizal traits (Chaudhary et al. 2022), which may constrain invasion success (Pringle et al. 2009) and/or be altered after invasion (Lekberg et al. 2013), can be inferred from hyperspectral data

at leaf (Jantzen et al. 2023) and canopy level (Sousa et al. 2021). Where remote sensing methods reach their limits, novel field-portable instruments and sensor networks are very promising tools to measure ecophysiological information at the individual plant level with very high temporal resolution (Tognetti et al. 2022).

Additionally, advances in wireless, autonomous microsensors, such as leaf wearable sensors of ecophysiological processes (Frey et al. 2023; Reimer et al. 2021), may offer novel sampling strategies. Currently, novel autonomous sensor networks are being developed (e.g. ECOSENSE, Werner et al. 2024; Allan et al. 2018; Besson et al. 2022; Tognetti et al. 2022), enabling high spatial coverage of different functional properties in heterogeneous environments with distributed sensors continuously recording at high temporal resolution. Autonomous sensing is coupled to wireless data transmittance and real-time data assimilation into large databases to streamline the information flow and enable real-time analysis. Though still in its infancy, these novel automated sensing networks may also provide valuable new insights in invasion ecology. Such standardized and automated networks of field sensors are required to validate proxies of ecosystem functioning derived from satellite data, particularly in heterogeneous ecosystems (Naethe et al. 2024). Clearly, challenges apply when sampling at such fine resolution regarding data volume, data heterogeneity, varying data quality, and timely data availability, which requires sophisticated data management and analysis (Farley et al. 2018), as well as appropriate sampling strategies. Despite all technological progress, trade-offs between resolution and extent of analysis will still apply. Nevertheless, these new technologies bear the potential to provide the high spatial coverage required in heterogeneous environments to quantify invader-ecosystem interactions and validate remote sensing data for model transfer and upscaling.

Integration: spatial modelling of functional changes and impact assessment across different stages of invasion

Integration of the information on functional changes by the invader, characteristics of the recipient community, and the environmental context from different sources and at different scales is needed to assess and predict the invader impact on ecosystem functioning along gradients of invasion in heterogeneous ecosystems (Figs 3, 4). Once the functional tracer of impact is identified, the spatio-temporal dimension of the impact is understood, and spatial layers of both ecosystem structure and invader distribution at appropriate scale are available, alterations of ecosystems in the neighbourhood of the invader can be mapped using spatial modelling approaches.

Novel technologies clearly facilitate data sampling at multiple resolutions (see above). This enables explorative analysis of species-environment interactions at multiple scales, which is essential when spatio-temporal dimension of the effect is not known (see Holland and Yang 2016). Integrative approaches include mixed-effect models (Golicz et al. 2023), which have been applied to map invader-ecosystem interactions (Hellmann et al. 2017). To assess model transferability, area of applicability, variable selection, and methods of cross-validation need to be carefully evaluated (Ludwig et al. 2023). Recording data with high spatio-temporal resolution will inevitably lead to large data sets. Again, machine learning approaches, in particular DL, have recently gained popularity to analyze complex spatio-temporal datasets (Wikle and Zammit-Mangion 2023). Within the field of ecology, the versatility of DL is evident (Christin et al. 2019; Hirn et al. 2022; Perry et al. 2022), with its primary utility likely lying in species identification and mapping

(Christin et al. 2019; Kattenborn et al. 2021; Borowiec et al. 2022; Müllerová et al. 2023). Further, methods of DL enable multi-trait retrieval across vegetation types even when data are scarce (Cherif et al. 2023). Recent progress also includes the retrieval of traits using hybrid models, which combine leaf-canopy-atmosphere radiative transfer modelling with Gaussian processes and enable upscaling of trait maps from the local to regional level, including uncertainty estimates (Estévez et al. 2022). Especially in earth system sciences, DL approaches have been used to model system states and analyze systems processes (Reichstein et al. 2019). Future progress regarding model interpretability and explainability is expected if data-driven approaches and physical models are combined (Reichstein et al. 2019), and concepts are developed for automated workflows and pipelines to study ecosystem dynamics (Besson et al. 2022). However, progress in automated data collections and analysis based on artificial intelligence is not a solution per se to answer questions in ecology. It also poses challenges, e.g. in terms of standards, protocols and workflows, data infrastructure and data quality. Thus, defining scope and scale to study ecological phenomena will still be required (de Koning et al. 2023).

In the following, we will use an example to quantify the impact of a N-fixing invader in a N-poor Mediterranean ecosystem as one efficient but not exclusive way to integrate spatio-temporal information and functional tracers for invader impact assessment (Fig. 4).

We used field-based maps of both a N-fixing invasive species and a functional tracer ($\delta^{15}N$), which were joined with airborne LiDAR data on topography (environmental context) and vegetation structure (recipient community) to model functional changes across sites and stages of invasion (Hellmann et al. 2017). Plotting these maps onto fused airborne LiDAR and true colour image data allows visualizing and communicating context-dependent invader-ecosystem interactions at the molecular level, which are otherwise undetectable. The nitrogen isoscapes in Fig. 4 are centred around a N-fixing invasive species and illustrate the effect of dynamic N enrichment by the invader (reddish colours) in a N-poor open dune ecosystem (indicated by the yellowish colours) in three-dimensional space. This N-fixing effect does not occur uniformly around the invader, but is shaped by vegetation structure and topography. This explains, for example, N-transfer from fixation into the non-N-fixing native vegetation (yellowish colours), and the flush of nitrogen into sparsely vegetated areas downhill from the invader, which will slowly be transformed into denser habitats.

Other integrative approaches include the combination of field-based and remotely sensed data on native and invasive species distributions, vegetation structure, Leaf Area Index, or evapotranspiration to, for example, estimate water consumption of an invader in riparian habitats (Nagler et al. 2009; Dzikiti et al. 2017). To transfer and validate approaches across landscapes, information on topography (environmental context) and species composition (recipient community) is deemed essential (Le Maitre et al. 2015).

In summary, the importance of linking ecophysiology with remote sensing data to understand invasion processes has been outlined (Niphadkar and Nagendra 2016), and integrative approaches on mapping invader-ecosystem interactions are at hand (Nagler et al. 2009; Dzikiti et al. 2016; Hellmann et al. 2017). Due to technological progress, automated systems to study ecosystem dynamics at unprecedented scales are being developed and implemented (Allan et al. 2018; Besson et al. 2022; Tognetti et al. 2022), with potential to build digital twins (de Koning et al. 2023) of plant invasion impact, i.e. dynamic virtual representations or models used for simulations

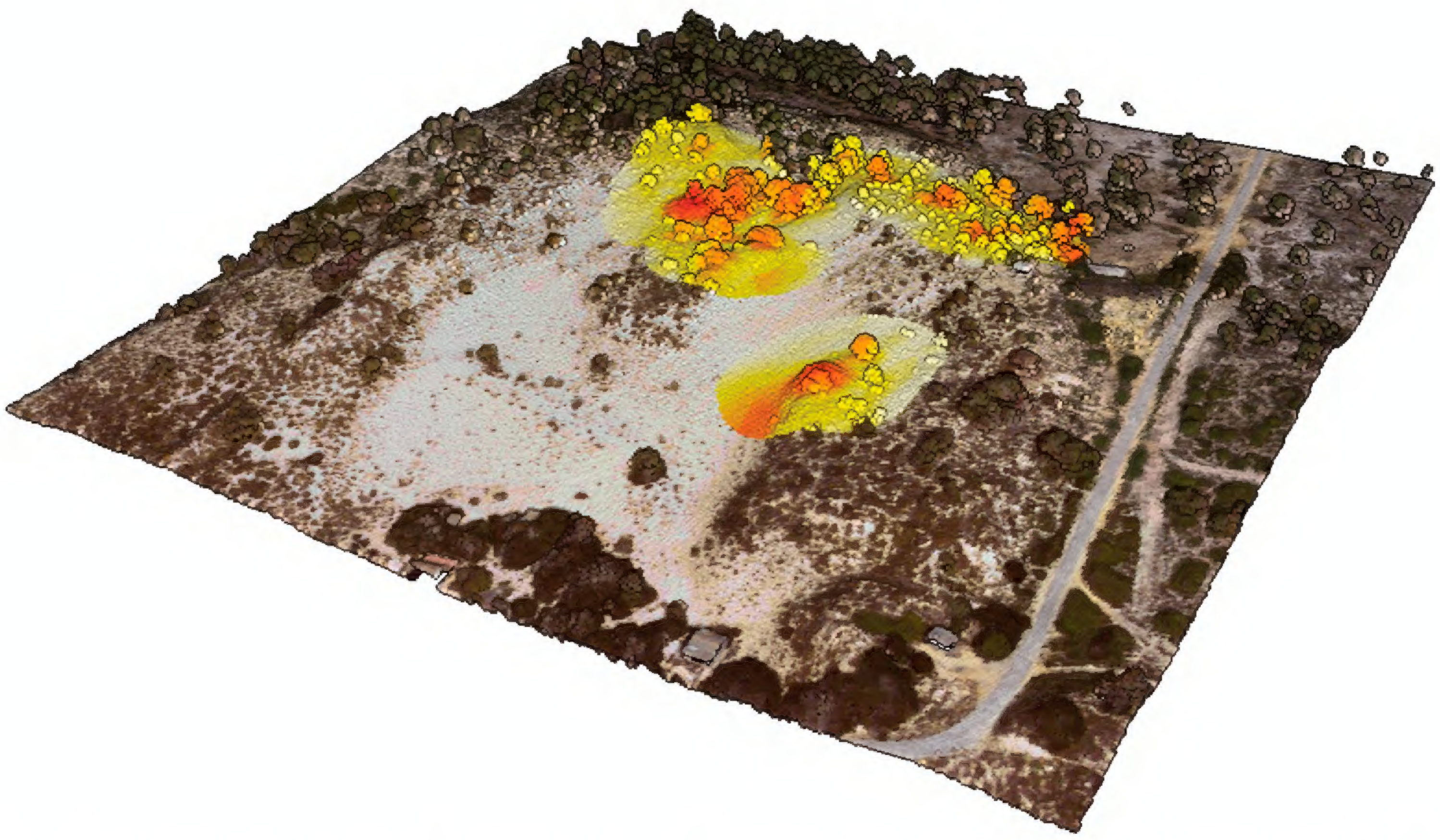

Figure 4. Model visualisation of spatio-temporal dynamics of invader impacts based on the suggested framework. Modelled isoscapes centred around a N_2-fixing invasive plant species using the functional tracer $\delta^{15}N$ and information on the environmental matrix in a nutrient poor ecosystem based on Hellmann et al. (2017). Reddish colours indicate high-levels of atmospheric fixed nitrogen inputs (e.g. dense invader patches and flushes of N into native vegetation); yellow colours indicate lower levels of impact, while whitish colours indicate no impact and are representative for the original status before invasion. The local functional changes do not occur uniformly. Isoscapes are plotted onto high-resolution airborne LiDAR data fused with true colour imagery to illustrate the effect of LiDAR-derived vegetation structure of the recipient community and topography on invader impact in this heterogeneous ecosystem. The 3D map was created using QGIS version 3.30. An animated 3D-video of the model can be found at https://tinyurl.com/4hs23b8p.

and analyses. We envision that these new approaches will also lead to advances in the field of biological invasions, namely to better understand fine-scale invader-ecosystem interactions, test invasion theories, and provide robust validation data for interactions across spatio-temporal dimensions in heterogeneous ecosystems.

Concluding remarks

Spatio-temporal patterns and variation of plant-plant interactions in heterogeneous environments deserve better integration in invasion research. Here we advocate the use of functional tracers for integrating fine-scale interactions between the invasive species, the recipient community, and the environmental context into spatial models to assess context-dependency of invader impact, namely the interplay of direct and indirect invasive-native species interactions. We advocate drawing on the large toolbox of recent methods, which when combined, can open new doors for mapping and predicting changes in ecosystem functioning and for assessing and disentangling the influence of spatio-temporal heterogeneity on invader impacts. By explicitly emphasizing the spatio-temporal variation of plant-plant interactions in invasion ecology, we anticipate major advances for understanding of invasion history, patterns of spread, impact assessment, and prediction of future invasions.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

All authors developed the framework. CH and CW wrote the first draft, which was revised by CW and AGS. AGS implemented the video animation.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Description of the animated video

Authors: Christiane Werner, Christine Hellmann, André Große-Stoltenberg

Data type: docx

Link: https://doi.org/10.3897/neobiota.94.126714.suppl1

Supplementary material 2

Animated video

Authors: Christiane Werner, Christine Hellmann, André Große-Stoltenberg

Data type: mp4

Link: https://doi.org/10.3897/neobiota.94.126714.suppl2